

SYSTEMATICS, PHYLOGENY, AND EVOLUTION OF *PAPAVER CALIFORNICUM* AND *STYLOMECON HETEROPHYLLA* (PAPAVERACEAE)

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ABSTRACT

We present a detailed comparison of *Papaver californicum* and *Stylomecon heterophylla*, which earlier were found to be sister species and most closely related to *Meconopsis cambrica* + *Papaver s.str.* from western Eurasia. The two species of winter annuals differ mainly in the shape of their distal cauline leaves, coloration of petals and staminal filaments, and most notably morphology of the gynoecium and capsule, with *Papaver californicum* having a sessile stigmatic disc and *Stylomecon heterophylla* having a distinct style. They were earlier found to differ in ploidy, with chromosome numbers of $2n = 28$ (*Papaver californicum*) and $2n = 56$ (*Stylomecon heterophylla*). Mapped distributions of the two species indicate that the range of *S. heterophylla* encompasses and exceeds that of *P. californicum*; both are known only from the California Floristic Province except for one collection of *S. heterophylla* from central Baja California. Whereas *Papaver californicum* is most commonly found in burn localities in the first wet season after fire, *Stylomecon heterophylla* is active under a broader range of environmental conditions and often occurs in habitats that appear to be somewhat more mesic. Both species are self-compatible and autonomously self-pollinating. Experimental hybridization resulted in well-developed but entirely sterile hybrids; no hybrids are known from nature. Based on these and earlier findings, we conclude that *Stylomecon heterophylla* is best treated in *Papaver*, as *P. heterophyllum*.

Key Words: *Papaver*, *Meconopsis*, *Stylomecon*, fire poppy, wind poppy, breeding system, capsule morphology, hybridization.

In the native flora of California, Papaveraceae *s.str.* (i.e., excl. Fumariaceae and Pteridophyllaceae, see Stevens 2001 onwards) are represented by two subfamilies, i.e., subf. Eschscholzioidae, with *Dendromecon* Benth. and *Eschscholzia* Cham., and subf. Papaveroideae, with *Arctomecon* Torr. & Frém., *Argemone* L., *Canbya* Parry ex A. Gray, *Hesperomecon* Greene, *Meconella* Nutt., *Papaver* L., *Platystemon* Benth., *Romneya* Harv., and *Stylomecon* G. Taylor. Whereas Eschscholzioidae are endemic to western North America (the third genus of the subfamily, *Hunnemannia* Sweet, is distributed in Mexico), the genera of subf. Papaveroideae fall into an Old World clade and a New World clade, respectively (Schwarzbach and Kadereit 1995). Of the genera of subf. Papaveroideae in California, *Papaver*, with the fire poppy, *P. californicum* A. Gray [syn. *P. lemmonii* Greene], as its only native species, and the monotypic *Stylomecon*, with only the wind poppy, *S. heterophylla* (Benth.) G. Taylor [basonym *Meconopsis heterophylla* Benth., syn. *Papaver heterophyllum* (Benth.) Greene], are part of the Old World clade (Schwarzbach and Kadereit 1995), which in addition to *Papaver* and *Stylomecon* contains the Old World genera *Meconopsis* Vig. and *Roemeria* Medik.

A close relationship between *Papaver californicum* and *Stylomecon heterophylla*, first suggested by Gray (1887), based on vegetative and reproductive characters, and by Greene (1888), upon combination of (at that time) *Meconopsis heterophylla* into *Papaver*, was also suspected by Ernst (1962) in view of the close vegetative similarity of the two species. A sister-species relationship between the two was first shown by Kadereit et al. (1997) using chloroplast DNA (cpDNA) restriction site data, and was confirmed by Carolan et al. (2006) using nuclear ribosomal DNA internal transcribed spacer (ITS) and cpDNA sequence data. Considering gynoecium and fruit morphology, however, the close relationship between the two species was unexpected. *Papaver californicum* has a gynoecium with a sessile stigmatic disc, and the capsules open by small valves (Fig. 1) below this stigmatic disc. Both of these characteristics are typical for *Papaver* in its traditional circumscription (Kadereit 1993). In contrast, the gynoecium of *S. heterophylla* has a distinct style on top of a flattened ovary roof, and the capsules open by pores below that roof (Fig. 1). Within Old World Papaveroideae, gynoecia with a style are typical for most species of *Meconopsis*, and this charac-

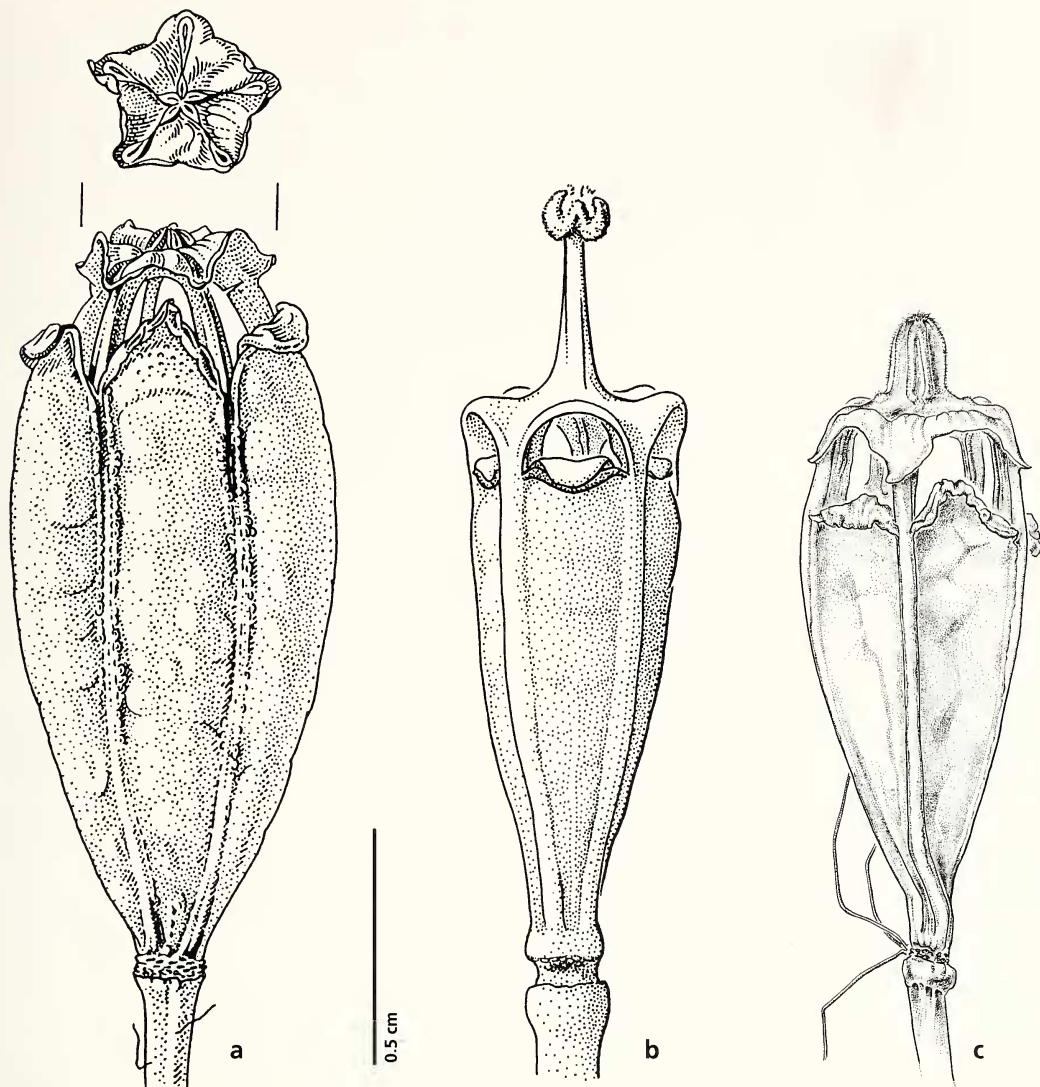


FIG. 1. Mature capsules of (a) *Papaver californicum*, (b) *Papaver heterophyllum* [*Stylomecon heterophylla*], and (c) their F_1 hybrid (*P. heterophyllum* \times *P. californicum* Rebman 15166).

teristic led Bentham (1835) to originally describe *S. heterophylla* as a species of *Meconopsis*.

From the perspective of the close relationship but morphological distinctness of *Papaver californicum* and *Stylomecon heterophylla*, we here set out to present a detailed comparison of the two species. Whereas a recent taxonomic account is available for *P. californicum* (Kadereit 1988), no such account exists for *S. heterophylla*, although *P. californicum* and *S. heterophylla* were briefly compared by Kadereit et al. (1997). In particular, we compare the two species in terms of morphology, karyology, and breeding system, and describe their geographical distributions and ecology. Finally, we briefly discuss their morphological evolution and the disjunction between

these two species and their closest relatives in the Old World.

METHODS

Sources and Cultivation of Living Material

Bulk seed was collected in California from one population of *Stylomecon heterophylla* (Contra Costa Co., Mt. Diablo, *S.J. Bainbridge s.n.* [JEPS], 2009) and two populations of *Papaver californicum* (San Diego Co., [1] Hellhole Canyon Open Space Preserve, E of Valley Center and NE of Lake Wohlford, 33.2256°N, 116.9443°W, 465 m. elevation, on mostly granitic substrates, *Rebman 15166* [SD], 14 May 2008, [2] Del Dios

Highlands County Preserve, SW of Escondido, NW of Lake Hodges and NE of Olivehain Reservoir, 33.0817°N, 117.1269°W, 242 m. elevation, granite and clay soils, *Rebman 15264* [SD], 23 May 2008).

Seeds were sown on moist filter paper in petri dishes and kept in a refrigerator at 5°C for about 14 days. Germination occurred readily in *Stylomecon heterophylla*, but required addition of 0.02% gibberellic acid in *Papaver californicum*. Seedlings or seeds were transplanted into pots and plants were cultivated in the experimental greenhouse at the Botanic Garden of Mainz University.

Breeding System and Hybridization

For the determination of breeding system, buds were bagged before opening, and seed set was checked at the time of capsule maturity. Four buds of *Stylomecon heterophylla* and seven buds of *Papaver californicum* were treated in this way. For interspecific hybridization, plants were emasculated before their anthers opened, and pollen of the crossing partner was applied to the stigmata once they became receptive. After pollination, the gynoecia were bagged and seed set was checked at capsule maturity. Twelve flowers of *S. heterophylla* and six flowers of *P. californicum* were used as female parents. Nine hybrid individuals were used in self-pollinations and inter-hybrid crosses.

Herbarium Material and Seed Morphology

All material of *Papaver californicum* and *Stylomecon heterophylla* in the University and Jepson Herbaria (UC/JEPS) was examined. For the distribution map of the two species, specimens in the Consortium of California Herbaria and, for Baja California, in UC and the San Diego Natural History Museum herbarium (SD) were used. The observations and descriptions presented below were based on both the cultivated and herbarium material. Scanning electron microscope pictures of gold-coated seeds were taken on an XL30 ESEM Philips (Philips Electron Optics, The Netherlands) microscope.

RESULTS

Morphology

Papaver californicum and *Stylomecon heterophylla* differ from each other in both vegetative and reproductive (flower and fruit) morphology. Both species are short-lived annuals with a flowering peak in March and April, but plants have been found flowering as early as February and as late as May. In cultivation at Mainz, Germany during late spring/early summer they required between 6 and 9 weeks to reach the onset of flowering from time of seed germination.

Although Ernst (1962) stated that "(t)heir seedling stages are identical, and even the adult plants are so similar in appearance that determinations cannot be made without the gynoecia", *Papaver californicum* and *Stylomecon heterophylla* can be easily distinguished by leaf morphology. The rosette and proximal cauline leaves of the two species indeed are very similar in appearance; however, the middle and distal cauline leaves of *S. heterophylla* are distinguished by their fine dissection (Fig. 2). The rather abrupt transition between proximal and middle cauline leaf margins and shapes in wind poppy probably account for Bentham's (1835) choice of the specific epithet 'heterophylla'.

The two species are conspicuously different in flower and fruit morphology. First, the flowers differ in coloration. The petals of *Papaver californicum* are pale orange with a distinct but small whitish to greenish and sharply delimited spot at the petal bases, and the staminal filaments are white to pale yellow; in contrast, the petals of *Stylomecon heterophylla* are bright orange with a small, dark red and distally fading spot at the petal bases, and the staminal filaments are dark red to almost black. Often the petals of *S. heterophylla* also are substantially larger than those of *P. californicum*, which often has very small, narrow, and sometimes irregularly lacinate petals. Second, the number of stamens, at least in the plants cultivated for this study, is greater in *S. heterophylla* than in *P. californicum*. These latter two differences, petal size and stamen number, may be associated with a slight difference between the two species in breeding system (see below). We also note that the flowers of our cultivated material of *S. heterophylla* were slightly zygomorphic: in the slightly nodding flowers, a distinctly larger number of stamens was displaced to the upper than to the lower side of the flower. Third, and most conspicuously, the two species differ in gynoecium and fruit morphology. Whereas *P. californicum* has a gynoecium with a sessile stigmatic disc, and capsules that open by small valves below this stigmatic disc (Fig. 1), the gynoecium of *S. heterophylla* has a distinct style on top of a flattened ovary roof, and the capsules open by pores below that roof (Fig. 1). Finally, the two species differ in seed size, at least in the material cultivated for this study. The seeds of *P. californicum* ranged from 607 to 649 μm in length; those of *S. heterophylla* had a mean length of 803 μm . Seed surface morphology is very similar in the two species, but surface microsculpturing is coarser in *P. californicum* than in *S. heterophylla* (Fig. 3).

Karyology

Ernst (1962) reported a chromosome number of $2n = 28$ for *Papaver californicum* and of $2n =$

Distribution

The geographic distribution of the two species is shown in Fig. 4. *Papaver californicum* is endemic to the western California Floristic Province (CA-FP) and known from the San Francisco Bay Area (Mt. Tamalpais vicinity and Mt. Diablo) of Central Western California south to northwestern Baja California, Mexico, with populations on Santa Cruz and Santa Rosa islands. Most known occurrences of fire poppy are documented from the South Coast, Transverse, and Peninsular ranges of California and from California's Central and South Coast, at elevations up to ca. 1220 m. The distribution of *S. heterophylla* encompasses the range of *P. californicum* and extends further north, south, and east, at elevations up to ca. 1500 m., with one record from outside the CA-FP, in the Vizcaino Desert of Baja California. Wind poppy is also known from all of the Channel Islands except San Nicolas Island and from near-shore Pacific islands of Baja California (Islas Los Coronados, Isla San Martin, and Isla Todos Santos). Wind poppy has been collected more extensively than fire poppy in Central Western California and northwestern Baja California, and is documented from the central and southern Sierra Nevada foothills, Tehachapi Mountains, and North Inner Coast Ranges (near Clear Lake), well outside the known range of fire poppy. The actual distribution of *P. californicum* is likely underrepresented by collections based on the infrequent appearance of plants, usually in the year immediately after fires (see below).

Ecology

Papaver californicum, as implied by its vernacular name, fire poppy, is most commonly found in burn localities in the first wet season after fire. However, the species occasionally also grows in otherwise disturbed or open sites (e.g., on cleared ground, *Brandege* 3372 [UC]; mesic openings in chaparral, *S. Boyd et al.* 6736 [UC]; dry open ridge, *I.W. Clokey & B. Templeton* 4464 [UC]; south facing boulder creek bed, *R. Ornduff & R.L. Taylor* 4389 [UC]; along newly-made truck trail, *R. Bacigalupi* 2876 [UC]).

The habitat of *Stylomecon heterophylla* is often but not exclusively described as moist and shady, and the species sometimes is found growing along streams. Soils are often described as loamy (e.g., soft sandy loam, clay loam, sandstone-derived clay-loam soil, leaf mold loam). In general, the habitat of this species often appears to be somewhat more mesic than that of *Papaver californicum*, although the ecological range of wind poppy extends into drier settings, as well (e.g., in Baja California). One specimen of *S. heterophylla* (*M.L. Bowerman* 1410 [UC]) origi-

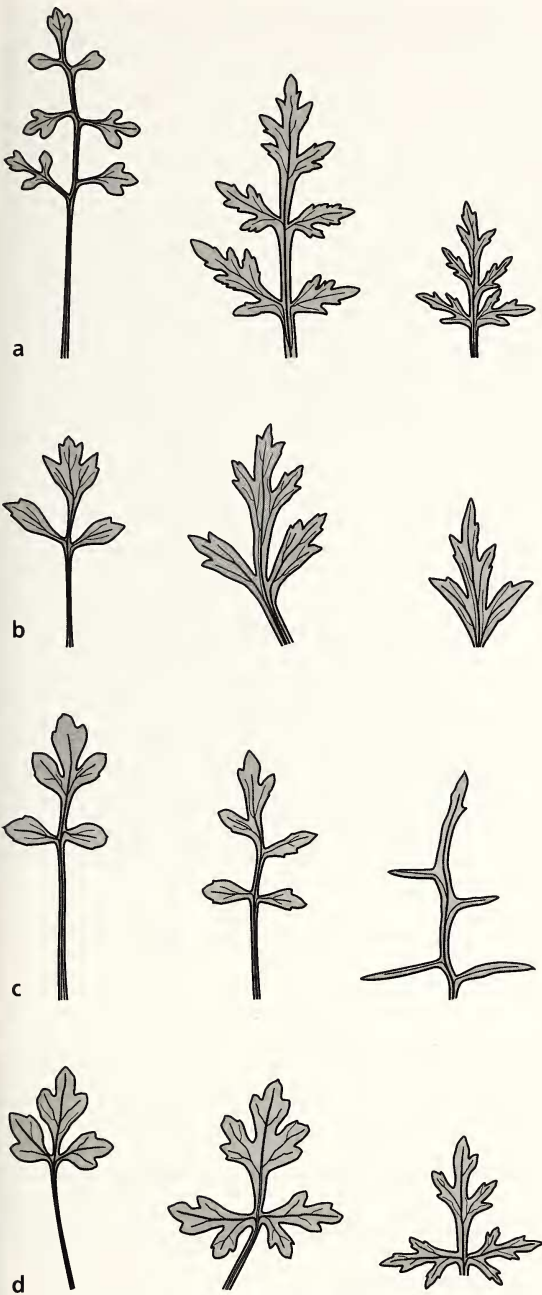


FIG. 2. Leaf shapes of (a, b) *Papaver californicum* (a: *Rebman* 15166, b: *Rebman* 15264), (c) *Papaver heterophyllum* [*Stylomecon heterophylla*], and (d) their F₁ hybrid (*P. heterophyllum* × *P. californicum* *Rebman* 15166). Left to right: rosette, proximal cauline, and distal cauline leaves.

56 for *Stylomecon heterophylla*. Considering that $x = 6$ and 7 are the lowest chromosome numbers found in *Papaver* and relatives (Kadereit 1993), *P. californicum* is interpreted here as tetraploid and *S. heterophylla* as octoploid.

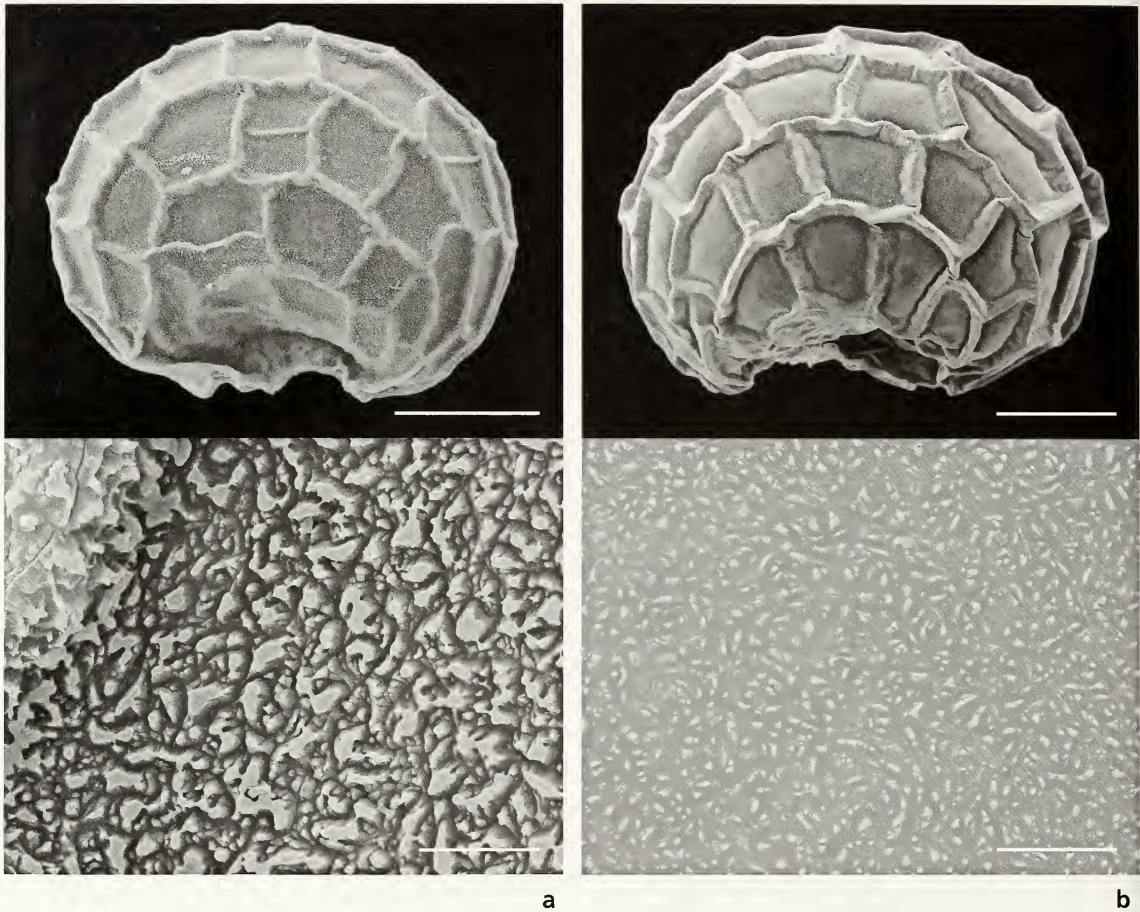


FIG. 3. SEM photographs of seeds (scale bars: 200 μm) and seed surface details (scale bars: 10 μm) of (a) *Papaver californicum* (Rebman 15264) and (b) *Papaver heterophyllum* [*Stylomecon heterophylla*].

nated from a site swept by fire in the previous year.

Breeding System

In the breeding-system experiment, all bagged flowers showed good seed set. Both species were thus determined to be self-compatible and autonomously self-pollinating. Their late floral development was found to differ, however. In *Papaver californicum*, stamens exceeded the gynoecium, anthers always opened in bud, and pollen was found on the stigmatic rays when the buds opened, although at that time the stigmatic rays appeared not to be receptive, as judged from the later appearance of stigmatic papillae. In *Stylomecon heterophylla*, the stigmata — elevated by the style — do not overtop the anthers in but are located at roughly the same level. The anthers were still closed when flower buds began to open. During opening of the anthers, some pollen is deposited on the stigmata, which, as in *P. californicum*, appeared not to be receptive at this stage.

Hybridization

Hybridization between *Papaver californicum* and *Stylomecon heterophylla* was successful only when *S. heterophylla* was the female parent, and all 12 crosses made in that direction resulted in seed set. Hybrid individuals developed normally but produced no seed when selfed or crossed with other hybrid plants. A hybrid capsule is shown in Fig. 1.

DISCUSSION

Phylogenetic Relationships, Evolution, and Biogeographical History of *Papaver californicum* and *Stylomecon heterophylla*

In their restriction site analysis of cpDNA, Kadereit et al. (1997) found *Papaver californicum* + *Stylomecon heterophylla* to be part of a polytomy with (1) the South African *P. aculeatum* Thunb., (2) a clade of *Papaver* sect. *Argemonidium* Spach + *Roemeria* Medik. as sister to *Papaver* sect. *Meconella* Spach, and (3) a clade

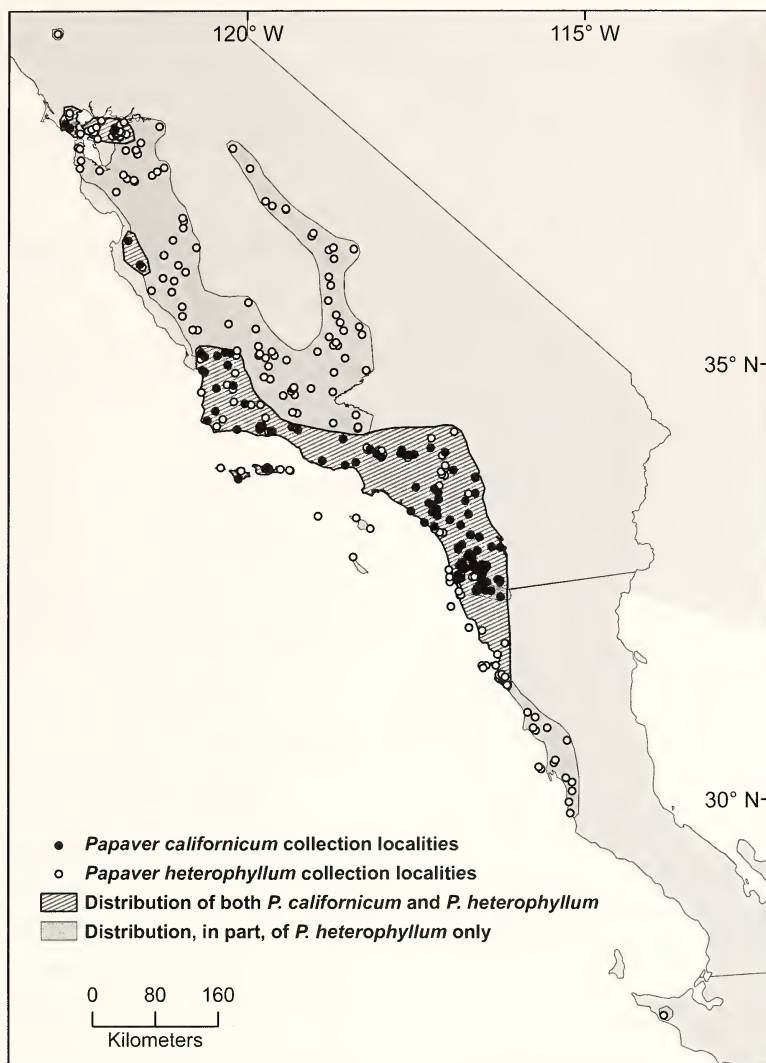


FIG. 4. Geographical distribution of *Papaver californicum* and *P. heterophyllum* [*Stylomecon heterophylla*].

of the western European *Meconopsis cambrica* (L.)Vig. as sister to *Papaver sensu stricto* (*s.str.*) as defined by Kadereit et al. (1997). Two lineages of Asian *Meconopsis* were successive sister groups to this polytomy, although without much support. In their analysis of ITS and cpDNA (*trnL-F*) sequence data, Carolan et al. (2006) recovered *P. californicum* + *S. heterophylla* as sister to *M. cambrica* + *Papaver s.str.* The remainder of those lineages listed above were found to be basally divergent to this clade. The sister-group relationship between the Californian *P. californicum* + *S. heterophylla* and the largely western Eurasian *M. cambrica* + *Papaver s.str.*, and the more basally divergent position of the remaining lineages was confirmed in an analysis of an enlarged ITS dataset by F. J. Valtueña Sánchez and J.W. Kadereit (unpublished). Phylogenetic relationships in Old World Papaveroideae as found by Kadereit et al.

(1997) and Carolan et al. (2006) are summarized in Fig. 5. A close relationship of *P. californicum* + *S. heterophylla* to *M. cambrica* + *Papaver s.str.* had already been suspected by Ernst (1962). When discussing the results of their phylogenetic analysis, Kadereit et al. (1997) hypothesized that *Meconopsis*, as a genus of mostly mesic habitats, is best interpreted as paraphyletic in relation to several lineages of a polyphyletic *Papaver* (including *Roemeria* and *Stylomecon*). Except for the arctic-alpine *Papaver* sect. *Meconella*, all of these lineages grow in semi-arid to arid habitats.

The above phylogenetic interpretation, which is consistent with the results of Carolan et al. (2006) and F. J. Valtueña Sánchez and J.W. Kadereit (unpublished), has several implications for the morphological evolution of the Californian *Papaver californicum* + *Stylomecon heterophylla* lineage. First, the annual habit of this

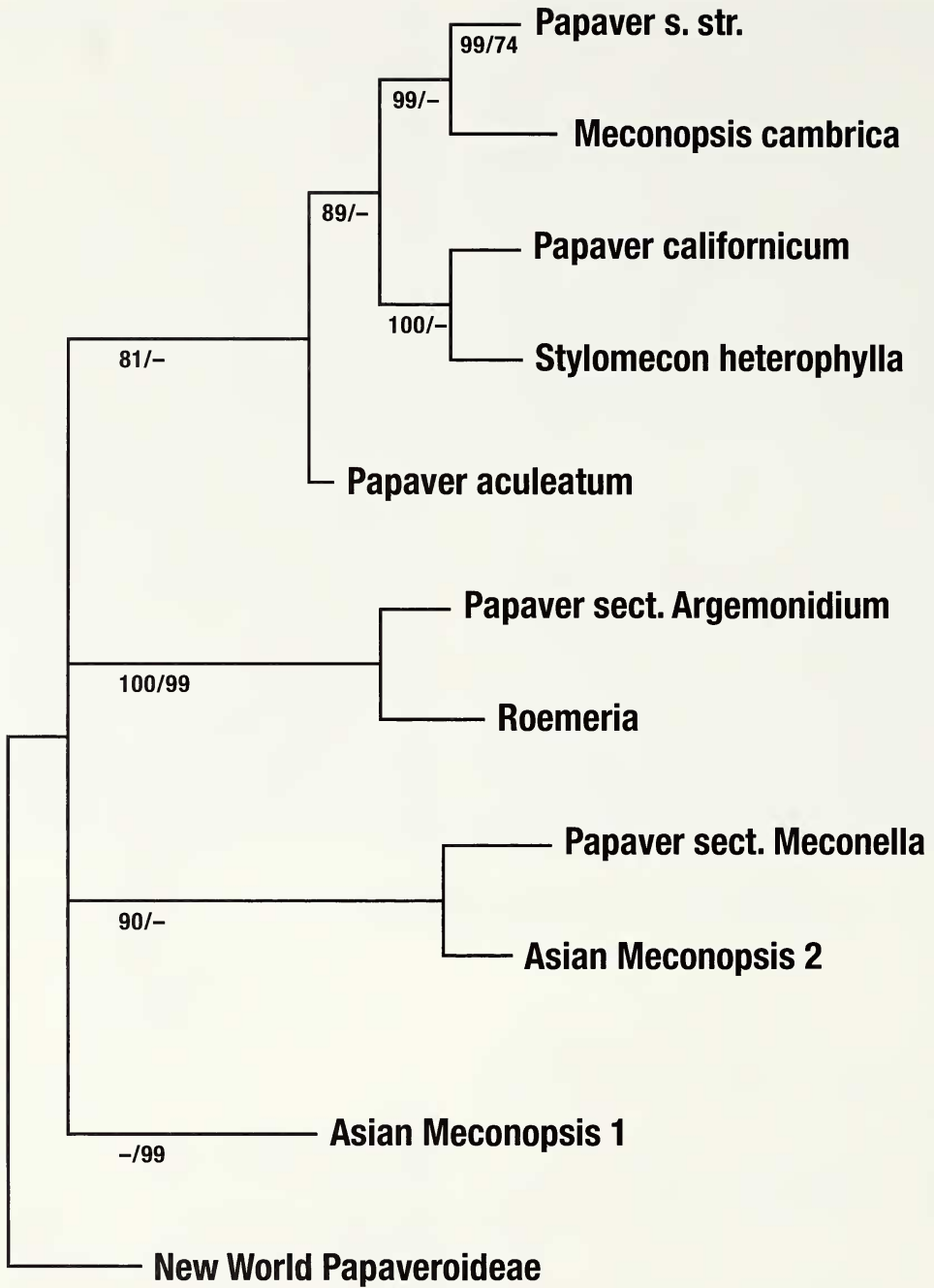


FIG. 5. Simplified phylogeny of Old World Papaveroideae based on Kadereit et al. (1997) and Carolan et al. (2006). Figures along branches represent bootstrap support found by Carolan et. al. (2006)/Kadereit et al. (1997).

lineage was likely derived from an ancestrally perennial condition, as found in *Meconopsis*, including *M. cambrica*, and large parts of *Papaver*. Second, the dark pigmentation of the filaments of *S. heterophylla* evolved independently from the similar coloration of filaments found in essentially all annual lineages of *Papaver s.str.*, in the perennial *Papaver* sect. *Macrantha* Elkan, and in the annual *Papaver* sect. *Argemonidium* +

Roemeria—filaments are light in much of *Mecconopsis*, including *M. cambrica*, and all biennial and perennial sections of *Papaver s.str.* except sect. *Macrantha* (Kadereit et al. 1997). Third, a distinct style, as present in *S. heterophylla*, is found only in some species of *Meconopsis*, including *M. cambrica*, and may not be strictly homologous across all of these taxa. Capsules with a stigmatic disc, as present in *P. californi-*

cum, are only found in the various lineages of *Papaver* discussed above. It is unclear from phylogenetic relationships alone whether the stigmatic disc of *P. californicum* arose in parallel to that of *Papaver s.str.*, or whether the style of *S. heterophylla* arose in parallel to that found in some members of *Meconopsis*, including *M. cambrica*. However, studies of gynoecium development (Kadereit and Erbar in press) support Ernst's (1962) conclusion that a distinct style may have arisen independently in different lineages of subf. Papaveroideae. Ernst (1962) questioned homology of gynoecium/capsule morphology in *Meconopsis*, including *M. cambrica*, and *Stylomecon*, particularly in light of capsule venation (see Kadereit et al. 1997 for detailed discussion). Accordingly, it seems most likely that the style of *S. heterophylla* arose from a structure similar to the stigmatic disc of *P. californicum*. The transition between gynoecia with and without styles results from the activity of a ring primordium located between the placentae and the carpel tips. Prolonged activity of this ring primordium results in the formation of a style (Kadereit and Erbar in press). As noted above, elevation of the stigmata by the style in *S. heterophylla* does not result in herkogamy and is not obviously associated with other floral characteristics of *S. heterophylla* that differ from those of *P. californicum* in ways that may indicate a stronger tendency toward outcrossing in wind poppies, with anthers not opening in bud and with generally larger petals and more stamens than in *P. californicum*.

The interpretation of *Meconopsis* as a paraphyletic grade basal to a polyphyletic *Papaver* (including *Roemeria* and *Stylomecon*) also has biogeographical implications. We hypothesize that the Californian lineage of *P. californicum* and *S. heterophylla* arose from an ancestral lineage of primarily mesic ecology and widespread northern hemisphere distribution. Based on a fossil-calibrated Bayesian analysis of divergence times, under a relaxed clock, using BEAST (Drummond and Rambaut 2007) with a large ITS data-set of Old World Papaveroideae, the split between *P. californicum* + *S. heterophylla* and *M. cambrica* + *Papaver s.str.* was dated to 18.3 (26.3 to 10.8) million years ago (mya) and the split between *P. californicum* and *S. heterophylla* to 13.4 (21.9 to 5.6) mya (F. J. Valtueña Sánchez and J.W. Kadereit unpublished). The disjunction between Old World and New World Papaveroideae would thus represent the geographical tail-ends of a formerly widespread northern hemisphere lineage, as found in several other flowering plant lineages (Kadereit and Baldwin in press). However, this hypothesis and an alternative hypothesis of long-distance dispersal as explanations for the disjunction between *S. heterophylla*/*P. californicum* and their Old

World sister group (*M. cambrica*/*Papaver s.str.*) cannot be tested further in the absence of fossil evidence.

Considering the estimated ancient timing of the split between *Papaver californicum* and *Stylomecon heterophylla*, it is remarkable that we obtained viable hybrids between these two species. Attempts at such hybridization by Ernst (1962) were not successful. Hybrid plants were morphologically distinctive, with intermediate gynoecium and capsule morphology (Fig. 1), although they resembled *P. californicum* in leaf shape (Fig. 2) and filament and petal coloration. No such plants were seen among all herbarium specimens investigated in this study. In nature, hybridization between the two species probably is limited by their different ecological requirements, either prezygotically, through lack of crossing opportunities, or postzygotically, through lack of survival of hybrids under field conditions. The extent to which their different ploidy levels, as opposed to other genetic or chromosomal factors (e.g., lack of chromosomal pairing) are responsible for sterility of hybrids between them, and thus strong postzygotic reproductive isolation, remains to be studied.

Taxonomic Consequences

Considering the well-supported sister-group relationship of *P. californicum* + *S. heterophylla* to *Meconopsis cambrica* + *Papaver s.str.* (Kadereit et al. 1997; Carolan et al. 2006; Fig. 5), the generic assignment of either *P. californicum* or *S. heterophylla* needs to be revised in order to achieve monophyletic taxa. Two options for accomplishing this goal are readily apparent. First, *P. californicum* could be combined into *Stylomecon*. Considering phylogenetic relationships in Old World Papaveroideae (Kadereit et al. 1997; Carolan et al. 2006; Fig. 5), this approach would require a) establishing a new genus for the South African *P. aculeatum*, b) including *Papaver* sect. *Argemonidium* in *Roemeria*, c) establishing a new genus for *Papaver* sect. *Meconella* or including this section of *Papaver* into part of Asian *Meconopsis*, and d) treating Asian *Meconopsis* as generically distinct (possibly in two genera) from the phylogenetically isolated, European *M. cambrica*, the type species of *Meconopsis*. Second, *S. heterophylla* could be combined into *Papaver*. This approach would require the treatment of *M. cambrica* in *Papaver* — the species was originally described as *P. cambricum* by Linnaeus — but would allow *P. aculeatum* to remain in *Papaver*. Treatment of the remaining lineages listed above (i.e., *P.* sect. *Argemonidium*, *P.* sect. *Meconella*, Asian *Meconopsis*, and *Roemeria*) would depend on their exact relationships to *Papaver s.str.* (including *M. cambrica* and *S. heterophylla*), which have not yet been

resolved with high support (Kadereit et al. 1997; Carolan et al. 2006). Both taxonomic options would result in genera with heterogeneous capsule morphology and probably also in genera that cannot easily be diagnosed morphologically. Based on evidence that the styler capsules of *M. cambrica* and *S. heterophylla* evolved independently and probably from ancestors with a *Papaver*-like stigmatic disc (Ernst 1962; Kadereit and Erbar in press) and on desirability of minimizing nomenclatural changes, we here follow the second option outlined above and treat *S. heterophylla* in *Papaver*, as *P. heterophyllum* (Benth.) Greene.

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